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6.

NOTE ON THE FUNCTIONAL AND STRUCTURAL ARRANGEMENT OF EFFERENT FIBRES IN THE NERVE-ROOTS OF THE LUMBO-SACRAL PLEXUS.

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"Note on the Functional and Structural Arrangement of Efferent Fibres in the Nerve-roots of the Lumbo-sacral Plexus." (Preliminary Communication.) By C. S. SHERRINGTON, M.A., M.B., &c. Communicated by Professor M. FOSTER, Sec. R.S. Received March 14, 1892.

At the commencement of some observations on the reflex mechanisms of the spinal cord in *Macacus rhesus*, difficulties were encountered which made it desirable to attempt for that animal a somewhat particular examination of the distribution of the efferent and afferent spinal nerve-roots belonging to the lumbo-sacral plexus. The present communication has reference to the distribution of the efferent fibres of the roots.

Reil,* Scarpa,† A. Monro,‡ and Soemmering§ all paid considerable attention to the arrangement of the root-bundles in the limb plexuses, but physiological work upon the subject commenced with Van Deen,‖ J. Müller,¶ and Panizza.** The former two gave an anatomical significance to the plexus, the last a physiological. At Müller's suggestion, renewed research was undertaken by H. Kronenberg†† in 1835. Kronenberg confirmed Müller's observations as to the individual inconstancy of the contribution made by any spinal root to the nerve cords of the plexus; he also concluded that the excitation of a single nerve-root before its entrance into the plexus produces contraction of almost all the muscles of the limb; and that the arrangement is intended to protect against fatigue. Later, Eckhardt,‡‡ working in Ludwig's laboratory, arrived at somewhat similar conclusions. He stated that a great number of muscles obtain nerve-fibres each of them from several nerve-roots; that there is a good deal of individual variation; that when a nerve-root is

* 'De Nervorum Structura,' p. 14.

† 'De Gangliis et Plexibus.'

‡ 'Observations on the Structure and Functions of the Nervous System,' p. 34.

§ 'Anatom.,' Pars Vta.

‖ 'De Differentia et Nexu inter Nervos Vitæ Anim. et Organ.,' Leyden, 1834.

¶ 'Physiol. des Menschen,' vol. 2, p. 586.

** 'Annali Universali di Medicina.'

†† Essay ('De Struct. et Virtut. Plexuum Nervorum'), Berlin, 1836.

‡‡ 'Zeits. f. Rat. Med.,' vol. 7, p. 306, 1849.

unusually thick the additional fibres in it are not all of them, perhaps none of them, used to supply the muscles usually supplied by the root, but are used to supply altogether other muscles not usually supplied by the roots; that the distribution of the fibres of a root is not to one group of muscles, but is to several groups, which are often not related to each other in function; that antagonistic groups are often supplied by one and the same root.

Three years after the experiments by Eckhardt, and also under Ludwig, Peyer's* experiments on the brachial plexus of the rabbit were made. As Krause, in 1861,† repeated Peyer's work on the same limb and the same species, the results of both may be here referred to together. The muscles of the limb each receive nerve-fibres from two, in some cases three, spinal roots; usually the contraction of a muscle on excitation of the spinal roots innervating it is obviously different in degree for each root: the same spinal root does not always supply in different individuals the same muscles; the further the position of a spinal root from the head, the nearer the muscles it supplies to the distal end of the limb; the peripheral trunks of the limb plexus are themselves plexuses of root-bundles. In 1881 Ferrier and Yeo‡ confirmed the above results in experiments on the spinal roots of the monkey. In addition to their experiments on the brachial plexus, they performed four complete experiments on the lumbo-sacral roots. Unlike Kronenberg, Eckhardt, and others, they do not seem to have met with any variation in the results obtained. They revived the view that the efferent distribution of each spinal nerve is based on its physiological function, and that the movement resulting from the excitation of a root is that of a highly coordinated functional synergism. Some months later Paul Bert and Marcacci§ published experiments on the lumbar roots of the cat and dog. They concluded that (i) each root produces a coordinate movement, and consists of fibres functionally associated; (ii) when a muscle is functionally divisible its root-supply is multiple.

In 1883 Forgue and Lannegrace‖ published a research on the limb plexuses of the cat, dog, and monkey. The 'Comptes Rendus'¶ of the following year contain their reports. As to the lower limb, their account is prefaced by a remark that the highest lumbar root of man is tripled in the dog and monkey. What species of monkey was used is not mentioned in the 'Comptes Rendus.' In *Macacus* the 5th lumbar root is analogous not to the 3rd of man, but to the 4th, and

* 'Arch. f. Rat. Med.,' II, vol. 4, p. 67, 1853.

† 'Beiträge zur Anat. der Oberen Extremität,' 1861.

‡ 'Roy. Soc. Proc.,' 1881.

§ 'Soc. de Biol.,' July, 1881.

‖ 'Gaz. Hebd. des Sci. Médic. de Montpellier,' 1883.

¶ 'Comptes Rendus,' 1884, vol. 98, pp. 829, 685, 1068.

to the 6th of the dog. The chief of their conclusions, drawn from examination of both limbs, are:—The majority of muscles are innervated by several roots. Excitation of a root determines in the muscles which it supplies a total, not a partial, contraction. The tributary fibres of the root are disseminated through the muscle supplied by it, and not "cantonnées" in a special zone of it. Each root has a muscular distribution almost absolutely constant in the animals of its own species. The functions of analogous roots differ very little in different mammalian species. Each root supplies muscles of very various, often of antagonistic, action. Excitation of a root gives a combined movement, but an artificial, not a functional. The roots that pass furthest into the member occupy the lowest position in the cord. The innervation of the two planes of flexors and extensors is not always symmetrical. The superficial layers are supplied before the deep.

Herringham,* by minute dissection of the human brachial plexus, and, therefore, under disadvantage from inability to distinguish clearly between afferent and efferent fibres, arrived nevertheless at facts and conclusions of great importance. He found much individual variation, but evidence of certain "laws." Thus: any given root-fibre may alter its position relative to the vertebral column, but will maintain its position relative to other fibres; of two muscles, or two parts of a muscle, that which is nearer the head end of the body tends to be supplied by the higher, that nearer the tail end by the lower, root; of two muscles, that nearer the long axis of the body tends to be supplied by the higher, that nearer the periphery by the lower, root; of two muscles, that nearer the surface tends to be supplied by the higher, that further from it by the lower, root.

Recently Langley,† in the course of a paper on the sweat nerves to the foot of the cat, refers to the movements of the limb produced by excitation of roots of sciatic plexus in that animal. He desired to ascertain whether the variation, which he finds considerable in the distribution of the sweat nerves (sympathetic system), has a correlative in the distribution of the nerves to the limb muscles. Like Kronenberg, Eckhardt, and Peyer, he finds that the movements resulting from stimulation of the same nerve-roots are not uniform, and that the want of uniformity goes hand in hand with want of uniformity in the root composition of the plexus, just such as displayed in Herringham's dissections.

My own observations have been made, during the past three years, chiefly on the lumbo-sacral roots of *Macacus rhesus;* also on the frog, rat, rabbit, cat, and dog, chiefly for the sake of comparing those types with *Macacus*. The animals have been deeply anæsthetised

* 'Roy. Soc. Proc.,' 1887.

† 'Jl. of Physiol.,' September, 1891.

with chloroform and ether. The excitations of the roots have been made in the spinal canal; the single root, or a component filament from it, has been isolated in the case of the lower roots of the cat and monkey, to a length 5, 6, or 7 cm., and lifted up by a silk ligature on to small platinum electrodes sheathed almost to the points. Series of weak induced currents have been used for excitation, one pint Daniell being in the primary of the ordinary physiological inductorium (R. Ewald's pattern). The secondary coil has usually been at a distance from the primary somewhat more than twice that at which a current was detectable by the tongue. Use has also been made of absolutely minimal stimuli, and largely of mechanical stimuli. For certain purposes, stimulation by quite strong electrical excitation has been used.

In these experiments it became clear that the frequency of individual variation, as regards the anatomical and physiological constitution of the efferent roots of the lumbo-sacral region, was great enough to demand the recognition of a "pre-axial" and a "post-axial" class of innervation for each muscle and movement. By pre-axial class of innervation is meant that the roots connected with the muscles and the movements are more pre-axial than the roots connected with the same muscles and the same movements in the post-axial class of innervation.

Thus, in the frog there is a pre-axial class of innervation for the hind limb, in which, for instance, the viith spinal root, as well as supplying the antero-internal thigh muscles, supplies the muscles on the front of the leg (tibialis anticus). There is a post-axial class in which the pretibial muscles are supplied by the viiith and ixth roots only. The post-axial class as measured in this way is the more usual. This may be merely because the above criterion, found convenient for distinguishing in any individual case the direction which the variation has taken in it, does not coincide with the mid point about which individual variation in the species is really oscillating.

By "pre-axial" and "post-axial" classes it is not intended to imply that in the range of individual variation one case is not more frequently exemplified than are others; it is only meant that so frequent is the variation that no one case is sufficiently predominant to warrant the choice of it as a "normal" type, and that therefore it is more correct to treat the composition of the plexus of the species as multiple and then for convenience divide it into classes. I have thought two classes, "pre-axial" and "post-axial," a distinction sufficient to observe in my present description. Just as in the frog, so in the other animals employed, the "pre-axial" and "post-axial" class of the plexus have both been exemplified by individuals of each species. In the rat, rabbit, cat, and dog, the 9th subthoracic root sometimes supplies the intrinsic muscles of the foot (post-axial innervation), some-

times does not, the 8th taking its place (pre-axial class of innervation) as well as supplying other fibres also. In the cat, in my own experiments, the post-axial class, as measured by the above standard, has contained a rather larger number of individuals (twenty-two out of thirty-nine).*

In experiments on *Macacus*, also, it early became clear that the types of innervation of the limb-muscles by the spinal roots are conveniently dealt with as two classes. In fifty-two individuals the reactions obtained place the majority (thirty-one) within a pre-axial class, the broad features of which are as follows:—

Pre-axial Class of Innervation.

No. of the root excited.	Movement produced.
1st Subthoracic ..	Retraction of abdominal wall, near umbilicus in front.
2nd ,, ..	Retraction of lower part of abdominal wall, flexion of hip, with some eversion, drawing up of testicle (stronger than with 3rd).
3rd ,, ..	Retraction of lowest part of abdominal wall drawing up of the testicle, flexion at hip, with marked rotation of thigh outwards and some adduction, some extension of knee.
4th ,, ..	Flexion at hip, extension at knee, adduction of thigh, eversion of thigh.
5th ,, ..	Flexion at hip, extension at knee, adduction of thigh, strong flexion at ankle, drawing up of outer edge of foot, flexion of hallux and digits.
6th ,, ..	Extension at hip, adduction of thigh, flexion at knee, extension at ankle, rotation of leg inwards, lifting of outer edge of foot, flexion of digits and hallux at terminal joint with (sometimes) adduction.
7th ,, ..	Extension at hip, with slight rotation outward of the thigh, flexion at knee, extension at ankle, flexion of digits and hallux with adduction of hallux, depression and adduction of root of tail, closure of anus.
8th ,, ..	Extension at hip, with slight rotation outward of the thigh, flexion at knee, extension at ankle, strong flexion and adduction of hallux, flexion of digits in "interosseal" position, closure and protrusion of anus, root of tail adducted and depressed, perineum pushed down.

* This agrees with the observations by Langley, *loc. cit.*

No. of the root excited.	Movement produced.
9th Subthoracic ..	Adduction of root of tail, which is drawn toward the side stimulated.
10th	Proximal half of tail drawn toward side stimulated.

No of root excited.	Muscle thrown into action.
1st Subthoracic ..	Quadratus lumborum, psoas parvus, external oblique, internal oblique, transversalis.
2nd ,, ..	Quadratus lumborum, psoas magnus, cremaster, external oblique, internal oblique, transversalis.
3rd ,, ..	Psoas, cremaster, iliacus, external oblique, internal oblique (lower part only), transversalis, pectineus, adductor longus, sartorius (upper part especially), vastus internus, and obdurator externus slightly.
4th ,, ..	Psoas, iliacus, pectineus, adductor longus, sartorius (lower part especially), vastus internus (> vastus externus), crureus, obturator, rectus femoris, vastus externus, gracilis.
5th ,, ..	Gracilis, vastus externus (> vastus internus), rectus femoris, vastus internus, crureus, adductor magnus, semimembranosus, tibialis anticus, tensor vaginæ femoris, peroneus longus (occasionally strongly), flexor longus hallucis (slight), flexor longus digitorum (slight), tibialis posticus (slight), extensor longus digitorum, extensor proprius hallucis.
6th ,, ..	Tibialis anticus, extensor longus digitorum, extensor hallucis, peroneus longus, peroneus brevis, extensor brevis digitorum, gastrocnemius external head (> internal head), internal head, tibialis posticus, flexor longus digitorum, flexor longus hallucis, semimembranosus (> semitendinosus), semitendinosus, biceps (slight, chiefly in deep portion), adductor hallucis, flexor brevis digitorum, adductor hallucis (slight), adductor minimi digiti, soleus (slight), plantaris, popliteus, gluteus medius, quadratus femoris.
7th ,, ..	Tibialis anticus, extensor longus digitorum. extensor proprius hallucis, peroneus longus.

No. of root excited.	Muscle thrown into action.
	slight (< peroneus brevis), peroneus brevis, gastrocnemius external head, internal head, plantaris, tibialis posticus, flexor longus digitorum, soleus, flexor longus hallucis, extensor brevis digitorum, flexor brevis digitorum, adductor hallucis, adductor minimi digiti, flexor accessorius, flexor brevis hallucis, flexor brevis minimi digiti, interossei and lumbricales, obturator internus, quadratus femoris, gemelli superior et inferior, pyriformis (the larger part of, especially the lateral part), deeper part of sphincter ani, semitendinosus, semimembranosus, biceps, adductor magnus (part of), popliteus, gluteus medius.
8th Subthoracic ..	Biceps (< than semimembranosus), semitendinosus (< than semimembranosus), semimembranosus, gluteus maximus, gluteus medius, gastrocnemius internal head (< than external), external head, soleus, adductor hallucis, flexor accessorius, adductor minimi digiti, adductor hallucis, obturator internus, quadratus femoris (slight), gemelli superior et inferior, pyriformis (small part, chiefly mesial), sphincter ani, flexor brevis hallucis, flexor brevis minimi digiti, lumbricales and interossei.
9th ,, ..	Sphincter vaginæ, obturator internus (slightly).

The remaining twenty-one individuals formed a "post-axial" class, with the following broad characters in common :—

Root.	Movement.
1st Subthoracic .. (1st lumbar)	Retraction of abdominal wall.
2nd ,, ..	Retraction of lower part of abdominal wall, drawing up of testicle, slight flexion at hip.
3rd ,, ..	Contraction of lower part of abdominal wall, drawing up of testicle (stronger than with 2nd), flexion at hip, slight flexion at knee, slight rotation outwards of thigh.
4th ,, ..	Drawing up of testicle (slight)?, contraction of lower part of abdominal wall, flexion at

Root.	Movement.
	hip, with adduction of thigh, extension at knee, slight rotation outwards of thigh.
5th Subthoracic ..	Flexion at hip, with adduction of thigh, extension at knee, drawing up of inner edge of foot, with slight flexion at ankle, and slight extension of hallux
6th ,, ..	Extension at hip, with adduction of thigh, flexion at knee, flexion at ankle, lifting of outer edge of foot, extension of toes, with adduction of hallux.
7th ,, ..	Extension at hip, flexion at knee, extension at ankle, tilting of outer edge of foot, flexion of digits, with strong adduction of hallux, depression of root of tail, slight rotation outward of the thigh.
8th ,, ..	Slight rotation outward of the thigh, extension at hip, flexion at knee, extension (very strong) at ankle, strong flexion and adduction of hallux, flexion of digits in "interosseal" position, contraction of anus, root of tail depressed and drawn to side stimulated.
9th ,, ..	Slight rotation outwards of the thigh, flexion of digits, perineum pushed down, contraction of anus, abduction of root of tail toward side stimulated.
10th ,, ..	Abduction of root of tail toward side stimulated.
11th ,, ..	Proximal two-thirds of tail drawn toward side stimulated.
12th ,, ..	Distal half of tail drawn toward side stimulated.
13th ,, ..	Tip of tail drawn toward side stimulated.

Post-axial Class.

1st Subthoracic ..	Quadratus lumborum, psoas parvus, external oblique, internal oblique, transversalis.
2nd ,, .	Quadratus lumborum, psoas magnus, cremaster, external oblique, internal oblique, transversalis.
3rd ,, ..	Psoas magnus, cremaster, iliacus, external oblique, transversalis (the lower part only

Root.	Movement.
	of the three latter), pectineus, adductor longus, sartorius.
4th Subthoracic ..	Psoas magnus, iliacus, pectineus, the adductor longus, gracilis (probably the rest of the adductor mass), sartorius, vastus internus, vastus externus, crureus, rectus fem. (slight), obturator externus.
5th ,, ..	Gracilis, adductor longus (slight), tensor vaginæ femoris, rectus femoris, vastus internus, vastus externus, crureus, tibialis anticus, peroneus longus, semimembranosus (these latter only slightly), extensor hallucis (very slight).
6th ,, ..	Part of adductor magnus, tibialis anticus, extensor longus digitorum, extensor hallucis, peroneus longus, peroneus brevis, short (intrinsic) extensors of the digits, abductor minimi digiti, gastrocnemius (both heads, but slight), popliteus, tibialis posticus, flexor longus digitorum, long flexor of the hallux, soleus, semimembranosus, plantaris, semitendinosus, biceps.
7th ,, ..	Adductor magnus, semitendinosus, semimembranosus, tibialis anticus, extensor longus digitorum, extensor propr. hallucis, peroneus brevis, peroneus longus, plantaris, popliteus, gastrocnemius (both outer and inner heads), tibialis posticus, flexor longus digitorum, soleus, long flexor of the hallux, short extensor (intrinsic extensor) of the digits and hallux, short and accessory flexors (intrinsic flexor) of the digits and hallux, abductor minimi digiti, the abductor hallucis, the adductor hallucis, large part of pyriformis, interossei and lumbricales, obturator internus, quad. fem. and two gemelli.
8th ,, ..	Biceps, semimembranosus, semitendinosus, gluteus medius, gastrocnemius (both heads), soleus, tibialis posticus, flexor longus digitorum, abductor hallucis, abductor natum, short and accessory flexor of the digits and hallux, adductor of the hallux, interossei and lumbricales, sphincter ani, sphincter vaginæ, small part of pyriformis, obtu-

Root.	Movement.
	rator internus, quad. fem. and the two gemelli.
9th Subthoracic ..	Short flexor of the digit and hallux, adductor of the hallux, interossei and lumbricales, sphincter vaginæ, obturator internus, sphincter ani.

The results of the experiments are in harmony with those of Eckhardt. Many of the muscles of the limb are supplied by three spinal roots, some by two; one alone, as far as I have yet observed, by a single root only. Individual variation is frequent. Excitation of the same spinal root not always throws into action the same muscles, even in individuals of the same species, sex, and approximate age; nor does it always produce the same movement, *e.g.*, *flexion* at knee followed excitation of 5th root in two individual instances. Analysis of the distribution of the component filaments of a root shows that in different individuals filaments which correspond in absolute position in the nerve-root do not correspond in function. Nevertheless, Herringham's "Law I" (quoted above) holds good for the outflow of fibres throughout considerable regions of the cord, although a sciatic plexus of the post-axial class may occur in the same individual as a brachial plexus of the pre-axial class, so that in its narrowest sense the "law" is not always applicable to great lengths of the cord. No exception has been found to it in the sense that an efferent fibre pre-axial in one individual to some particular other efferent fibre is ever in any individual of the same species post-axial to it.

The distribution of the peripheral nerve-trunks is not obviously different, whether by its root-formation the plexus belong to the pre-axial or to the post-axial class. The peripheral nerve-trunks are, as regards their muscles, relatively stable in comparison with the spinal roots. When the innervation of the limb-muscles is of the pre-axial class, so also is that of the anus, vagina, and bladder; and conversely.

The region of outflow from the spinal cord of the fibres destined for a natural group of the limb-muscles, or the representation of a particular movement at a limb joint, is often not conterminous with the origin of the filaments of a spinal root, but has its limits at points within spinal segments, either overstepping or falling short of their boundaries. Thus the outflow to the intrinsic muscles of the sole sometimes has its upper limit placed nearly midway up the region of origin of the filaments of the 6th root. The lower limit of the outflow to the calf muscles sometimes lies about two-thirds down the region of origin of the 8th root. Other examples could be cited. The ankle, knee, &c., which seem to be divisions between funda-

mentally distinct portions of the limb, are not regarded as such in the segments of the spinal cord.

If the simple movements (flexion, &c.) of the limb-joints be considered individually, the region of representation in the spinal roots of *Macacus* extends for each into at least three segments of the cord. The region of representation for each simple movement is about as extended for the small joints (digits) as for the large (hip-knee). The whole region of representation for the movements of the knee is, however, longer (includes more cord segments) than that for the ankle; and that for the hip is longer than that for the knee. This is because the more distal the joint the greater the overlap of the regions of representation in the roots of each of the two opposed movements at the joint. Of the opposed movements, the one which is in a direction toward the anterior aspect of the limb is always represented the more pre-axially in the spinal roots.

In the thigh, the nerve-roots supplying the musculature are none of them common at once to the muscle groups of the anterior and posterior aspects of the thigh. In the foot and leg the nerve-roots supplying the muscles each supply muscles situated both on the anterior and posterior aspects; this is more marked in the case of the foot than of the leg; yet in the former even the musculature of the sole is distinctly post-axial to that of the dorsum.

Although there is clear evidence that the nerve supply of the skin of the hallux is pre-axial to that of the 5th digit, my experiments have given only equivocal evidence that the musculature of the hallux is pre-axial to that of the minimus; nor is in the thigh the gracilis (lower part) pre-axial to the vastus externus. The mutual relationship of gracilis and vastus externus is as that of rectus abdominis to erector spinæ in the trunk, *i.e.*, ventral to dorsal; the same is probably true of hallux and 5th digit (as regards their musculature). This is in accord with Paterson's* views of the mutual relationship of the obturator and anterior crural nerves, although not with his extension of a similar view to the relationship of the internal and external popliteal nerves.

The posterior aspect of the thigh and leg afford an important exception to the rule given by Forgue and Lannegrace, and confirmed, as regards the fore-limb, by Herringham, viz., that, of the superficial and deep muscular layers of a region of the limb, the superficial layer is innervated by more pre-axial roots than the deep layer. The reverse holds good for the calf muscles and the hamstrings.

The significance of the distribution of the efferent fibres of a spinal root is, as J. Müller suggested, anatomical (based on motamerism, &c.) rather than functional (based on co-ordinate action, &c.). Excitation of an entire efferent root produces a combined movement

* 'Jl. of Anat. and Physiol.,' 1887 and 1889.

due to the action of many muscles, but there is no safe ground for believing that the combination is of a functional character; the weight of evidence is against this.

As to the question whether a muscle, when supplied by several nerve-roots, is supplied by them in such a way that one piece of the muscle is supplied by one root, another by another, although there is certainly great interlapping of regions belonging to the individual roots, I cannot agree with Forgue and Lannegrace when they say, "Excitation of a spinal root determines in the muscles which it supplies a total, not a partial, contraction." Simple inspection is enough to convince one, that in the case of some of the larger muscles, *e.g.*, in the thigh and spinal regions, the nerve supply from the individual roots is distinctly partial, that a district of the muscle belongs to this root, another district to that, although always with a large mutual overlap; striking examples are given by the *sartorius*, 3rd and 4th (*Macacus*) *sacrococcygeus superior*, 7th, 8th, 9th (cat), &c. On the other hand, as the distal end of the limb is approached, the intermingling of the root-districts in the several muscles becomes more intimate, and in the muscles of the sole the intermingling of the muscle-fibres belonging to individual nerve-roots is so complete as to baffle analysis, except by the degeneration method. In the sphincter muscle of the anus there is an overlap of the motor distributions of the right and left halves of the body. The sphincter ani is supplied by four nerve-roots, two right-hand, two left-hand. Any three of these may usually be cut through without the anus becoming patulous, or exhibiting asymmetry. Conversely, excitation of any one of the efferent roots supplying it causes contraction of both right and left halves of it. The innervation of the bladder from its right- and left-hand roots, is, on the other hand, neither in the case of its sympathetic nor its direct spinal supply of a bilateral character.

HARRISON AND SONS, PRINTERS IN ORDINARY TO HER MAJESTY, ST. MARTIN'S LANE.